

2007

Ecological consequences of early Late Pleistocene megadroughts in tropical Africa

Andrew S. Cohen

Jeffrey R. Stone

See next page for additional authors

Follow this and additional works at: <https://digitalcommons.uri.edu/gsofacpubs>

Terms of Use

All rights reserved under copyright.

Citation/Publisher Attribution

Cohen, A. S., Stone, J. R., Beuning, K. R., Park, L. E., Reinthal, P. N., Dettman, D., Scholz, C. A.,...Ivory, S. J. (2007). Ecological consequences of early Late Pleistocene megadroughts in tropical Africa. *Proc. Natl. Sci. USA*, 104(42), 16422-16427. doi: 10.1073/pnas.0703873104

Available at: <https://doi.org/10.1073/pnas.0703873104>

This Article is brought to you for free and open access by the Graduate School of Oceanography at DigitalCommons@URI. It has been accepted for inclusion in Graduate School of Oceanography Faculty Publications by an authorized administrator of DigitalCommons@URI. For more information, please contact digitalcommons@etal.uri.edu.

Authors

Andrew S. Cohen, Jeffrey R. Stone, Kristina R. M. Beuning, Lisa E. Park, Peter N. Reinthal, David Dettman, Christopher A. Scholz, Thomas C. Johnson, John W. King, Michael R. Talbot, Erik T. Brown, and Sarah J. Ivory

Ecological consequences of early Late Pleistocene megadroughts in tropical Africa

Andrew S. Cohen^{*†}, Jeffery R. Stone[‡], Kristina R. M. Beuning[§], Lisa E. Park[¶], Peter N. Reinthal^{||}, David Dettman^{*}, Christopher A. Scholz^{**}, Thomas C. Johnson^{††}, John W. King^{‡‡}, Michael R. Talbot^{§§}, Erik T. Brown^{††}, and Sarah J. Ivory[§]

Departments of ^{*}Geosciences and ^{||}Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721; [‡]Department of Geosciences, University of Nebraska, Lincoln, NE 68588; [§]Department of Biology, University of Wisconsin, Eau Claire, WI 54702; [¶]Department of Geology, University of Akron, Akron, OH 44325; ^{**}Department of Earth Sciences, Syracuse University, Syracuse, NY 13244; ^{††}Large Lakes Observatory and Department of Geological Sciences, University of Minnesota, Duluth, MN 55812; ^{‡‡}Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882; and ^{§§}Department of Earth Sciences, University of Bergen, N-5007 Bergen, Norway

Edited by David Hodell, University of Florida, Gainesville, FL, and accepted by the Editorial Board August 27, 2007 (received for review April 30, 2007)

Extremely arid conditions in tropical Africa occurred in several discrete episodes between 135 and 90 ka, as demonstrated by lake core and seismic records from multiple basins [Scholz CA, Johnson TC, Cohen AS, King JW, Peck J, Overpeck JT, Talbot MR, Brown ET, Kalindekaffe L, Amoako PYO, et al. (2007) *Proc Natl Acad Sci USA* 104:16416–16421]. This resulted in extraordinarily low lake levels, even in Africa's deepest lakes. On the basis of well dated paleoecological records from Lake Malawi, which reflect both local and regional conditions, we show that this aridity had severe consequences for terrestrial and aquatic ecosystems. During the most arid phase, there was extremely low pollen production and limited charred-particle deposition, indicating insufficient vegetation to maintain substantial fires, and the Lake Malawi watershed experienced cool, semidesert conditions (<400 mm/yr precipitation). Fossil and sedimentological data show that Lake Malawi itself, currently 706 m deep, was reduced to an ≈125 m deep saline, alkaline, well mixed lake. This episode of aridity was far more extreme than any experienced in the Afrotropics during the Last Glacial Maximum (≈35–15 ka). Aridity diminished after 95 ka, lake levels rose erratically, and salinity/alkalinity declined, reaching near-modern conditions after 60 ka. This record of lake levels and changing limnological conditions provides a framework for interpreting the evolution of the Lake Malawi fish and invertebrate species flocks. Moreover, this record, coupled with other regional records of early Late Pleistocene aridity, places new constraints on models of Afrotropical biogeographic refugia and early modern human population expansion into and out of tropical Africa.

cichlid evolution | Lake Malawi | Out-of-Africa Hypothesis | paleoclimate | paleolimnology

Long, continuous records of Pleistocene paleoecological change in Africa are rare, despite their importance for addressing paleoclimatic, biogeographic, and evolutionary controversies in the tropics (1, 2). For Africa, understanding of Pleistocene environmental history comes from a variety of wetland, lake core, and outcrop records (3–7), which are of geologically short duration and/or low stratigraphic resolution, as well as from analyses of deep-sea cores (8, 9), which integrate information from large areas. To evaluate hypotheses about environmental history at the landscape scale (≈10⁴–10⁶ km²), and their potential influence on species' distribution and diversification histories (10), there is a need for records that merge the continuity and duration of deep-sea cores with the relatively rapid sedimentation and high temporal resolution found in lakes.

Here we describe paleoecological results from drill cores recently collected at Lake Malawi, a large (29,500 km²), deep (706 m) African rift lake located in the southern African tropics (9°–14°S). Today, Lake Malawi lies close to the southern extent of the Intertropical Convergence Zone. The lake's watershed experiences a mesic climate, with highly seasonal rainfall [800–2,400 mm/yr (11)]. Lowland vegetation is dominated by wet Zambezian woodlands, replaced by evergreen and then montane forests with increasing elevation (12). Lake Malawi itself is hydrologically open,

drained by the Shire River, although 82% of total water loss is through evaporation (13). It is currently a dilute (240–250 μS/cm conductivity), stratified water body, with negligible nutrient concentrations in surface waters, leading to very high water clarity (14).

In 2005, we collected drill cores from two sites in Lake Malawi (15, 16). The deep-water central basin, site 1 (11°17.66'S, 34°26.15'E, 592 m water depth) was drilled to provide a relatively complete record even during extreme low-lake stands. Four cores were retrieved from this site, one of which (MAL05-1C, 76 m in length) forms the basis for this study. The north basin, site 2 (10°01.06'S, 34°11.16'E, 361 m) was located where earlier studies (4) had shown the potential for a high-resolution record covering the last ≈100 ka. Seismic data indicating deep-water unconformities and low-stand deltas, plus total organic carbon/total inorganic carbon, saturated bulk density, and faunal data from the deeper site, yield a coherent record of extremely low lake levels (–550 to –600 m relative to modern water depths) from ≈135 to 127 ka, and again from 115 to 95 ka, with lake levels rising in a stepped and sometimes reversing fashion thereafter and reaching near-modern levels ≈60 ka (16). This occurrence of unprecedented megadroughts was manifested as well in our shallower drill site in Lake Malawi and in long core records from Lake Tanganyika and from Lake Bosumtwi in West Africa (16). In contrast to the extreme low lake levels experienced in the early Late Pleistocene, the aridity of the LGM appears to have been much less severe, with lake levels on the order of 30–200 m below modern from ≈35 to 15 ka (17). The present study demonstrates the profound ecological consequences of these extreme drought intervals and discusses their implications for both lacustrine species flock evolution and anatomically modern human demography and expansion out of Africa.

Results

Screen-Washed Samples (Fig. 1). Ostracodes. Low-diversity ostracode assemblages were found in several intervals of core 1C before 62 ka. All of these assemblages are exclusively benthic/epibenthic taxa that cannot survive under conditions of sustained lake floor anoxia, a condition that currently exists in Lake Malawi in water depths >200–250 m (14). Fossil transport from a shallower water source to deep water can be discounted, given the extreme fragility of the ostracode fossils and because the anoxic part of the lake is under-

Author contributions: A.S.C., K.R.M.B., C.A.S., T.C.J., J.W.K., and M.R.T. designed research; A.S.C., J.R.S., K.R.M.B., L.E.P., P.N.R., D.D., C.A.S., T.C.J., J.W.K., M.R.T., E.T.B., and S.J.I. performed research; A.S.C., J.R.S., and K.R.M.B. analyzed data; and A.S.C., J.R.S., K.R.M.B., and P.N.R. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. D.H. is a guest editor invited by the Editorial Board. Abbreviations: DCA, detrended correspondence analysis; LGM, Last Glacial Maximum; PAR, pollen accumulation rate; PCA, principal components analysis.

[†]To whom correspondence should be addressed. E-mail: cohen@email.arizona.edu.

This article contains supporting information online at www.pnas.org/cgi/content/full/0703873104/DC1.

© 2007 by The National Academy of Sciences of the USA

most of the last 60 ka. Because of their ability to take refuge from predators by vertical migration into anoxic and/or low-light, deep-water habitats (23), they are particularly abundant in stratified tropical lakes, and the abundance of their fossils is correlated with the extent of lake-floor anoxia above a core site (24).

Charred particles. Charred-particle abundance varies over four orders of magnitude in the core 1C record, providing an excellent indicator of fire frequency near the drill site. Between ≈ 115 and 96 ka, charcoal abundance drops to near zero (largely corresponding with the *Limnocythere* ostracode-dominated lake interval), pointing to a period of extreme aridity, when the landscape converted periodically to semidesert, with disconnected plant cover and limited fuel beds incapable of sustaining major fires. In southern Africa, the modern precipitation threshold for fire-sustaining fuel beds is ≈ 400 mm/yr (25), suggesting that precipitation was this low or lower during the no-charcoal phase of the megadrought. Charcoal abundance rises dramatically after 96 ka, reaching near-modern (pre-20th century) levels by ≈ 60 ka, with a minor drop during the LGM.

Principal components analysis (PCA). Data from PCA of screen-washed samples [see [supporting information \(SI\) Text](#) and SI Table 1 for mineralogy data] yields a coherent picture of paleoecological change at Lake Malawi over the last ≈ 150 ka (Fig. 1). The first PCA axis (PC1) for all analyzed variables (those displayed plus those from ostracode taphonomy results, percentage adults, percentage broken valves, and percentage whole carapaces) explains 32.3% of the data variance and contrasts strongly positive loading variables (percentage *Limnocythere* spp., percentage total ostracode abundance, percentage adult ostracodes, and percentage broken valves) with strongly negatively loading variables (chaoborid, charcoal, and vivianite abundance). These results show that PC1 is primarily a lake-level/watershed moisture availability axis, consistent with the illustrated paleolake-level constraints (16) that can be placed either on the core or on Lake Malawi itself for the last ≈ 150 ka. Prolonged low lake levels and aridity occurred between 105 and 95 ka, with shorter episodes at ≈ 111 –108 ka and ≈ 127 –132 ka. Low stands are associated with shoreline indicators that lake level had dropped at least to the core site elevation. Lesser episodes of aridity are indicated by smaller peaks after the main megadrought period ended, from 95 until ≈ 60 ka. In contrast, the LGM, a time of well documented aridity throughout tropical East Africa (26, 27), is manifested by only a very small rise in PC1 scores, consistent with the much smaller lake-level decline at that time.

Diatoms. Light microscopy revealed a diverse diatom assemblage, with 112 taxa enumerated. All assemblages are dominated by plankton and tychoplankton (accidental plankton) forms, and abrupt transitions in the dominant species are common (Fig. 2). Stratigraphically constrained cluster analysis quantitatively defined eight zones, which conform to major shifts in the axis of maximum variance as determined by detrended correspondence analysis (DCA) (DCA1; 13% of total variance) (see [SI Tables 2 and 3](#)). DCA1 sample scores are typically high before ≈ 85 ka and low after ≈ 74 ka.

Diatom zones D-1 to D-4 (150–85 ka). Diatom zones D-1 and D-3 are dominated by *Aulacoseira* species that are common at low abundances in modern Lake Malawi (28–30). Increased abundances of *Aulacoseira* species in the modern lake are often associated with shallower water environments and higher silicate concentrations in the water column (14, 31–33). The dominance of *Aulacoseira* species before ≈ 85 ka suggests that the lake was much shallower and more frequently mixed than today. Diatom zones D-1, D-3, and D-4 are characterized by the highest DCA1 scores, associated with increased abundances of *Cyclotella meneghiniana*. This taxon has never been reported as abundant in the modern flora of Lake Malawi but occurs elsewhere today in East Africa in saline or moderately alkaline, nitrogen-rich waters (34–36). In large lakes, it tends to dominate the nearshore plankton when chloride inputs are

high and salinity levels fluctuate rapidly (37). The presence of this species as a common component of fossil assemblages suggests saline waters associated with drastically lower water depths.

Gradual increases in abundance of *C. meneghiniana* in the upper half of zones D-1 and D-3 suggest fluctuating salinity and low silicate concentrations associated with rising lake levels and less frequent mixing. Abundant *Stephanodiscus* species and the abrupt disappearance of *C. meneghiniana* throughout most of zone D-2 indicate deeper lake conditions than those observed in zone D-4, where *C. meneghiniana* remains the dominant form throughout and waters probably remained somewhat saline. The appearance of *Cyclotella ocellata*, a facultative plankter often considered to be littoral, at the top of zone D-2 suggests declining lake levels. Although there are no modern analogues in East Africa where *C. ocellata* is a dominant taxon, fossil assemblages rich in *C. ocellata* have been reported from Lakes Abhé and Tanganyika, where it was associated with water depths ranging from 100 to 150 m (38, 39). **Diatom zones D-5 to D-8 (85–10 ka).** The upper four diatom zones differ markedly from the lower four zones, as illustrated by the negative shift in DCA1 scores. This transition coincides with the disappearance of *C. meneghiniana* and *C. ocellata* at the top of D-4, an abrupt increase in the relative abundance of *Stephanodiscus* species, and gradual increases in other species that are common in low abundances in the modern and Holocene flora of Lake Malawi (28–30). These transitions suggest a shift toward much higher lake levels. Lake levels continued to fluctuate widely throughout zones D-5 and D-6 but never fell to the levels observed in the lower four diatom zones. Zones D-7 and D-8 show a decrease in sample-to-sample variability and a gradual increase in the abundances of *Stephanodiscus* species, suggesting that lake levels continued to rise and that the stratification of the lake became more pronounced, resulting in less frequent mixing of the water column.

Palynology. Between 120 and 75 ka, the pollen record shows a predominance of grass, with diverse yet sparsely represented arboreal, herbaceous, and wetland components surrounding Lake Malawi (Fig. 3 and see [SI Table 4](#)). Pollen spectra include both deciduous and evergreen arboreal taxa (*Celtis*, *Acalypha*, and *Moraceae*), as well as representatives from a lowland Zambezi miombo woodland ecosystem (*Brachystegia*, *Uapaca*, *Isobertinia*, and *Faurea*). Particularly striking is the relatively high pollen accumulation rate (PAR) values for *Podocarpus* and other montane indicators such as *Ericaceae*, *Olea*, *Juniperus*, and *Ilex*. Within this interval, *Podocarpus* PAR and percentages even exceed *Poaceae* at selected depths (35–38%), and the combined montane taxa represent an average of 20% of the grains deposited at the core site. In contrast, at no time during the last 35 ka did *Podocarpus* pollen percentages exceed 12% of the total pollen (ref. 40 and the present study). Samples from within the *Podocarpus* forest of the Drakensburg Mountains contain only $\approx 40\%$ *Podocarpus* pollen (41). These data, in conjunction with our results, strongly suggest substantial expansion of montane forest taxa to lower elevations within the highlands north and west of Lake Malawi (42). Such expansion would require cooler conditions, at least seasonally. The combined pollen and charred-particle data suggest that an ecosystem similar to the high-elevation semideserts of South Africa today probably existed near the lake shore, with expanded montane forests at higher elevations (43).

The substantial changes in total PAR after 105 ka inversely mirror the terrigenous component (percentage sand fraction) of sediment, with accumulation rates falling by an order of magnitude when Lake Malawi was very shallow. Because sedimentation rates do not increase along with the increase in sand, the decline in PAR at these times probably is not due to dilution or grain degradation but instead reflects a real change in pollen productivity and/or transport to the coring site. The percentage of broken/crumpled grains remains $\approx 8\%$ throughout the entire 120- to 75-ka interval.

From 105 to 95 ka, PARs fall to an average of <250 grains per

eration given their probable different responses to the megadrought (Tanganyika 800–1,000 m deep, moderately saline, extensive rocky coastal habitat assuming a near-modern basin configuration, possibly subdivided into multiple basins; Malawi, 100 m deep and saline, little rocky habitat, subdivided at times; Victoria, no record but probably dry) and the LGM arid phase [Malawi and Tanganyika, closed and undivided deep basins with abundant rocky habitat; Victoria, dry (27)] (see *SI Text and SI Fig. 5* for further discussion).

Our terrestrial ecological record, when coupled with other regional records of widespread southern tropical African aridity during the megadrought interval, has additional implications for early Late Pleistocene human demography and archaeology in Africa. The Lake Malawi record shows a shift from a period of high-amplitude climate variability between 140 and 70 ka, with at least two distinct episodes of desert-like conditions in tropical Africa, followed by a period of lowered variability over the last 70 ka, with generally more humid climates throughout that period, including the somewhat arid LGM (16). Whereas extreme variability in African climate regimes before 70 ka has been reported elsewhere in subSaharan Africa, it has primarily been in the context of unusually wet conditions [e.g., dated high stand deposits in the Kenyan rift (6)], in contrast to our evidence for extreme aridity. This interregional variability will make it difficult to identify specific region(s) (e.g., centers of modern forests) as persistent Afrotropical refugia throughout the Middle/Late Pleistocene. More likely, refugia themselves migrated in parallel with the intense climate swings, consistent with genetic evidence for chimpanzees (58). In this regard it is noteworthy that, simultaneous with the peak period of tropical African aridity [recorded at Lakes Malawi, Tanganyika, and Bosumtwi (16) and in the records of expanding deserts and active dune fields in both West Africa and the northern Kalahari (44–46)], abundant evidence exists for human occupation in southern and northern Africa, as well as in the Levant, whereas directly dated sites in tropical Africa are rare (59–62). The long African lake core records also make it less likely that the period of minimal human populations in equatorial Africa can be linked to events occurring after 80 ka (63). Furthermore, we propose that the expansion of more humid climate biomes is consistent with most models of both human and chimpanzee population expansion (64–67). The end of arid conditions in tropical Africa closely coincides with the onset of aridity elsewhere on the continent and in the Levant (9, 68, 69). Thus, a likely period for human population expansion out of equatorial Africa (especially up a Nilotic corridor from tropical to North Africa) would have been during the climatic “crossover” time, between ≈ 90 and 70 ka, when intermediate precipitation regimes would have prevailed throughout Africa. This interval is long enough to accommodate a zone of contiguous habitability during a genetic “sweep” up the Nile (65) and early enough to accommodate even early proposed arrivals of humans into Australia (70). It is also consistent with the idea (71) that the earlier (≈ 125 ka) documented occurrence of modern humans in North Africa and the Levant represents ultimately unsuccessful “excursions” out of Africa.

Methods

Core collection, geochronology, and archiving are described elsewhere (15, 16). After splitting, core MAL05-1C was sampled at 16-cm intervals (≈ 300 -yr resolution) for screen-wash and diatom analysis and at 1-m intervals for pollen samples. In total, 467 samples were collected for screen-wash and diatom analysis and 40 for palynology.

Screen-Washed Samples. Weighed wet sediment samples were disaggregated in deionized water and sieved using a 125- μm stainless steel sieve. Wet weights were determined for a separate aliquot from each sample, which was oven-dried and reweighed to determine water content and to calculate original dry weights for sieved samples. After sieving, residues were counted at $90\times$ for ostracodes [total number per sample, taphonomic condition (percentage adult, broken, carbonate coated, and reduction/oxidation stained), percentage major genera based on 100 valve counts, charred particles (total abundance per sample), chaoborid fragments, and percentage mineralogy in sand fraction]. Fossil identifications were confirmed by using a Philips (Eindhoven, The Netherlands) XL30 environmental scanning electron microscope. Fossil abundance, taphonomic, and mineralogic data from the screen-wash fractions were analyzed by PCA using CANOCO 4.5 (72). First axis PCA scores were smoothed by using a five-point running average of stratigraphically adjacent samples.

Diatoms. Diatom samples were prepared from all samples for light microscope analysis by using standard sample digestion, extraction, and mounting techniques (73). Clay-rich samples were immersed briefly (15–30 s) in an ultrasonic water-bath to disaggregate the sample and allow for complete digestion. When possible, a minimum of 300 diatom valves was identified from each sample interval; highly dissolved or sparse samples with <100 diatom valves counted were excluded from statistical analyses, leaving 463 samples.

Diatom percentage abundance data were screened to remove species that did not occur in abundances of at least 1% in two samples. After the screening, percentage abundance data for the remaining 51 diatom species were square-root transformed and analyzed by stratigraphically constrained cluster analysis (CONISS) using PSIMPOLL 4.10 (74) and by DCA using CANOCO 4.5 (72).

Palynology. Sediment samples (0.5 cm^3) were processed for pollen, in accordance with standard methods (75). Before final dehydration, a calibrated micropolystyrene spike was added to each sample to allow calculation of pollen concentrations (76). For each sample, 600 identifiable grains were counted. Identified grains were grouped into vegetation types on the basis of habitat preference of the parent plant. PARs were determined as number of grains per square centimeter per year, using mean pollen concentrations and the combined depth–age model.

We thank the University of Rhode Island and Lengeek Vessel Engineering, Inc., for general contracting and barge modifications during the Lake Malawi Scientific Drilling Project; the marine operations and drilling crews of the drilling vessel *Vipha*, provided by ADPS Ltd. and Seacore Ltd., respectively; DOSECC, Inc., Malawi Department of Surveys, Malawi Lake Services, and A. E. Oberem for logistical support; the scientific participants for field operations; the government of Malawi for permission to undertake this research; D. Gauggler, R. Markus, and L. Brooke McDonough for help with sample preparation; K. Behrens-meyer, A. Brooks, E. Michel, J. Todd, C. Tryon, D. Verschuren, C. Labandeira, and P. Wigand for valuable discussions; and two anonymous reviewers for many helpful comments. Funding for the field program was provided by the U.S. National Science Foundation–Earth System History Program and the International Continental Scientific Drilling Program, with additional funding for A.S.C. from the Smithsonian Institution (Evolution of Terrestrial Ecosystems Program and Fellowship Program). Initial core processing was carried out at LacCore, the National Lake Core Repository at the University of Minnesota.

1. Fjeldsaa J, Lovett JC (1997) *Biodivers Conserv* 6:325–346.
2. Linder HP (2001) *J Biogeogr* 28:169–182.
3. Jolly D, Taylor D, Marchant R, Hamilton A, Bonnefille R, Buchet G, Riollet G (1997) *J Biogeogr* 24:492–512.
4. Johnson TC, Brown ET, McManus J, Barry S, Barker P, Gasse F (2002) *Science* 296:113–132.

5. Talbot MR, Johannessen T (1992) *Earth Planet Sci Lett* 110:23–37.
6. Trauth MH, Maslin MA, Deino A, Strecker MR (2005) *Science* 309:2051–2053.
7. Cerling TE, Harris JM, MacFadden BJ, Leakey MG, Quade J, Eisenmann V, Ehleringer JR (1997) *Nature* 389:153–158.
8. Dupont LM, Jahns S, Marret F, Ning S (2000) *Palaeogeogr Palaeoclimatol Palaeoecol* 155:95–122.

9. DeMenocal PB (2004) *Earth Planet Sci Lett*, 220:3–24.
10. Potts R (1998) *Yearb Phys Anthropol* 41:93–136.
11. Malawi Department of Surveys (1983) *National Atlas of Malawi* (Blantyre, Malawi).
12. White F (1983) *The Vegetation of Africa* (UNESCO, Paris).
13. Owen RB, Crossley R, Johnson TC, Tweddle D, Kornfield I, Davison S, Eccles DH, Engstrom DE (1990) *Proc R Soc London Ser B* 240:519–533.
14. Patterson G, Kachinjika O (1995) in *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa*, ed Menz A (Natl Resources Inst, Chatham, UK), pp 1–67.
15. Scholz CA, Cohen AS, Johnson TC, King JW, Moran K (2006) *Sci Drilling* 2:17–19.
16. Scholz CA, Johnson TC, Cohen AS, King JW, Peck JA, Overpeck JT, Talbot MR, Brown ET, Kalindekafu L, Amoako PYO, et al. (2007) *Proc Natl Acad Sci USA* 104:16416–16421.
17. Barker P, Gasse F (2003) *Quat Sci Rev* 22:823–837.
18. Plisnier P-D, Chitamwebwa D, Mwape L, Tschibangu K, Langenberg VT, Coenen E (1999) *Hydrobiologia* 407:45–58.
19. Cohen AS, Dussinger R, Richardson J (1983) *Palaeogeogr Palaeoclimatol Palaeoecol* 43:129–151.
20. Palacios-Fest MR, Alin SR, Cohen AS, Tanner B, Heuser H (2005) *J Paleolimnol* 34:51–71.
21. Park LE, Cohen AS, Martens K, Bralek R (2003) *J Paleolimnol* 30:127–138.
22. Irvine K (1995) in *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa*, ed Menz A (Natl Resources Inst, Chatham, UK), pp 109–140.
23. Rine HE, Kesler DH (2001) *J Freshwater Ecol* 16:145–150.
24. Rumes B, Eggermont H, Verschuren D (2005) *Hydrobiologia* 542:297–314.
25. Bird M, Veenendaal E, Lloyd J (2004) *Global Change Biol* 10:342–349.
26. Bonnefille R, Chalief F (2000) *Global Planet Change*, 26:25–50.
27. Johnson TC, Scholz CA, Talbot MR, Kelts K, Ricketts RD, Ngobi G, Beuning K, Ssemmanda I, McGill JW (1996) *Science*, 273:1091–1093.
28. Hecky RE, Kling HJ (1987) *Arch Hydrobiol* 25:197–228.
29. Haberyan KA, Mhone OK (1991) *Hydrobiologia* 215:175–188.
30. Gasse F, Barker P, Johnson T (2002) in *The East African Great Lakes: Limnology, Palaeolimnology, and Biodiversity*, eds Odada EO, Olago DO (Kluwer, The Netherlands), pp 393–414.
31. Owen RB, Crossley R (1992) *J Paleolimnol* 7:55–71.
32. Kilham P, Kilham SS, Hecky RE (1986) *Limnol Oceanogr* 31:1169–1181.
33. Pilskaln CH, Johnson TC (1991) *Limnol Oceanogr* 36:544–557.
34. Blin DW (1993) *Ecology* 74:1246–1263.
35. Fritz SC, Cumming BF, Gasse F, Laird KR (1999) in *The Diatoms: Applications to Environmental and Earth Sciences*, eds Stoermer EF, Smol JP (Univ Press, London), pp 41–72.
36. Gasse F (1986) *East African Diatoms: Taxonomy, Ecological Distribution* (Cramer, Berlin), Bibliotheca Diatomologica, Vol. 11.
37. Tuchman ML, Theriot E, Stoermer EF (1984) *Arch Protistenkd* 128:319–332.
38. Gasse F, Ledée V, Massault M, Fontes JC (1989) *Nature* 342:57–59.
39. Gasse F, Street FA (1978) *Palaeogeogr Palaeoclimatol Palaeoecol* 24:279–325.
40. DeBusk GH (1994) PhD thesis (Duke Univ, Durham, NC).
41. Scott L (1989) *S Afr J Bot* 55:107–116.
42. Meadows ME (1984) *J Biogeogr* 11:209–222.
43. Scott L (1982) *Quat Res* 17:339–370.
44. Nichol JE (1999) *Geogr J* 167:79–89.
45. Thomas DS, Shaw PA (2003) *Quat Sci Rev* 21:783–797.
46. Pokras EM, Mix AC (1987) *Nature* 326:486–487.
47. Sturmhuber C, Baric S, Salzburger W, Rüber L, Verheyen E (2001) *Mol Bio Evol* 18:144–154.
48. Kocher TD (2004) *Nat Rev Genet* 5:288–298.
49. Seehausen O, van Alphen JJ, Witte F (1997) *Science* 277:1808–1811.
50. Scholz CA, King JW, Ellis GS, Swart PK, Stager C, Colman SM (2003) *J Paleolimnol* 30:139–150.
51. Danley PD, Kocher TD (2001) *Mol Ecol* 10:1075–1086.
52. Sturmhuber C, Hainz U, Baric S, Verheyen E, Salzburger W (2003) *Hydrobiologia* 500:51–64.
53. Duftner N, Koblmüller S, Sturmhuber C (2005) *J Mol Evol* 60:277–289.
54. Delvaux D (1995) in *Annual Report of the Department of Geology and Minerals, 1993–1994* (Royal Museum for Central Africa, Tervuren, Belgium), pp 99–108.
55. Scholz CA, Rosendahl B (1988) *Science* 240:1645–1648.
56. Cohen AS, Lezzar KE, Tiercelin J-J, Soreghan MR (1997) *Basin Res* 9:107–132.
57. Won Y, Wang Y, Sivasundar A, Raincrow J, Hey J (2006) *Mol Biol Evol* 23:828–837.
58. Goldberg TL (1998) *Intl J Primatol* 19:237–254.
59. McBrearty S, Brooks AS (2000) *J Hum Evol* 39:453–563.
60. Walter RC, Buffler RT, Bruggemann JH, Guillaume MM, Berhe SM, Negassi B, Libsekal Y, Cheng H, Edwards L, von Cosel R, et al. (2000) *Nature* 405:65–69.
61. Stringer C (2003) *Nature* 423:692–695.
62. Grün R, Stringer C, McDermott F, Nathan R, Poral N, Robertson S, Taylor L, Mortimer G, Eggins S, McCulloch M (2005) *J Hum Evol* 49:316–334.
63. Ambrose SH (1998) *J Hum Evol* 34:623–651.
64. Rogers AR (2000) *Evolution (Lawrence, Kans)* 49:608–615.
65. Harpending H, Rogers A (2000) *Annu Rev Genomics Hum Genet* 1:361–385.
66. Eswaran V, Harpending H, Rogers AR (2005) *J Hum Evol* 49:1–18.
67. Goldberg TL (1996) PhD thesis (Harvard Univ, Cambridge, MA).
68. Jacobs Z, Duller GAT, Wintle AG, Henshilwood CS (2006) *J Hum Evol* 51:255–273.
69. Tchernov A (1998) in *Neandertals and Modern Humans in Western Asia*, eds Akazawa T, Aoki K, Bar-Yosef O (Plenum, New York), pp 77–90.
70. Thorne A, Grün R, Mortimer G, Spooner NA, Simpson JJ, McCulloch M, Taylor L, Curnoe D (1999) *J Hum Evol* 36:591–612.
71. Klein R (1999) *The Human Career* (Univ Chicago Press, Chicago).
72. ter Braak C, Smilauer P (2002) *CANOCO 4.5* (Microcomputer Power, Ithaca, NY).
73. Battarbee RW (1986) in *Handbook of Holocene Palaeoecology and Palaeohydrology*, ed Berglund B (Wiley, New York), pp 527–570.
74. Bennett KD (2007) *Manual for psimpoll and pscomb Programs for Plotting and Analysis* (Queen's Univ, Belfast, Northern Ireland). Available at www.chrono.qub.ac.uk/psimpoll/psimpoll.html.
75. Faegri K, Iversen J (1989) *Textbook of Pollen Analysis* (Wiley, Chichester, UK).
76. Maher L (1981) *Rev Palaeobot Palynol* 32:153–191.